THE VISUAL SYSTEM OF THE GIANT CLAM *TRIDACNA:* BEHAVIORAL ADAPTATIONS

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ABSTRACT

Giant clams in the genus *Tridacna* exhibit a number of visual behaviors adapted to the hypertrophied siphonal lobes and the symbiotic zooxanthellae. The visual system consists of many eyes located along the margin of the siphon. Shadows without abrupt changes in intensity or movement elicit slow retractions of corresponding siphon regions. A similar response also occurs in isolated tissues and appears to rely on peripheral synaptic interactions. Otherwise, a shadow response, or a sight reaction to distant movements, triggers a synchronous rapid retraction of the entire siphon along with adduction of the valves. These abrupt responses are centrally coordinated and have a startling effect on would-be predators due to the water jetted from the exhalent aperture and the visual effect of movement by the large, brightly colored siphon. Animals become habituated to repetitive shadows but remain sensitive to stimuli of different spatial or temporal characteristics, thus illustrating the existence of complex central integrative mechanisms. A behavioral reflex to a light stimulus is also described whereby the surface of the mantle is directed toward the light. This 'orientation response' may represent a phototropic behavior which maximizes the absorption of light by the algal symbionts.

INTRODUCTION

Giant clams of the genus *Tridacna* are prominent members of tropical Indo-Pacific coral reef communities. Five species with overlapping ranges are widely distributed throughout the region (Rosewater, 1965). As the largest representatives of the bivalve molluscs, they exhibit a number of specialized adaptations and these are directly reflected by their habitat preference for relatively shallow (maximum depth, 20 m; Hardy and Hardy, 1969), clear, tropical seas. Most importantly, *Tridacna* hosts the photosynthetic endosymbiotic zooxanthella *Symbiodinium* (Freudenthal, 1962), and has come to rely on the algal photosynthates as a source of metabolic carbon (Trench *et al.,* 1981). In effect, *Tridacna* farms the zooxanthellae in large numbers in the tissues of its hypertrophied mantle siphon, the lobes of which are deployed past the shell margin and intentionally exposed to the intense solar radiation of the tropical marine environment.

In this 'farming' posture, the siphonal lobes are unprotected by the shell and, as observed by Stasek (1965), are subject to predation by reef fish. In his paper, Stasek describes generally the protective behavioral adaptations of *Tridacna,* including powerful spurts of seawater from the siphon apertures which can be directed toward the source of a tactile stimulus. A similar spurting reflex is mediated visually, presumably by the mantle eyes (Stasek, 1966), although a directional component has yet to be

demonstrated for this stimulus modality. Visually mediated behaviors include the shadow response, a withdrawal reflex common to most bivalves (Land, 1968), and the "sight reaction" in which reflex withdrawals are produced by moving objects even though their shadows fall to one side of the animal (Stasek, 1965). The shadow response of *Tridacna* is well known to the casual observer of the reef environment, including collectors and sport divers (Kawaguti and Mabuchi, 1969), and brief descriptions or anecdotes have been reported in the *Tridacna* literature by other authors (McMichael, 1974; Yonge, 1980; Fankboner, 1981).

The repertoire of *Tridacna* visual responses is further described in this report. Direct recordings of shell and mantle movements are used to analyze these behaviors. A sequence of increasingly more complex responses is presented ranging from local retractions, which also occur in isolated pieces of the mantle, to coordinated retractions of the entire siphon in concert with partial valve adductions. In addition, a novel phototrophic behavior is described which appears to facilitate maximal light absorption by the mantle, and which illustrates the capability for spatial resolution by the visual system.

MATERIALS AND METHODS

Several species of *Tridacna* were used in this study. Specimens of *T. maxima, T. squamosa,* and *T. derasa* were collected at Davies Reef, a platform reef on the Great Barrier Reef in N. Queensland off the coast from Townsville, Australia. The burrowing tridacnid *T. crocea* was collected from fringing reefs at the Palm Islands north of Townsville. Field observations were made with the aid of SCUBA on Davies Reef, and on Harold's Cay (Flinders Group) in the Coral Sea. Laboratory facilities were provided by the Australian Institute of Marine Science (AIMS) at Cape Ferguson and aboard the RV *Sirius* (February, 1981) and RV *Lady Basten* (June, 1981). Additional experiments were performed on small animals maintained in sunlit marine aquaria in Canberra.

Behavioral recordings

Movements of the shell and mantle of *Tridacna* were recorded by means of dual-arm strain gauge transducers and bridge circuits constructed in the laboratory and powered by 6 V batteries. In one series of experiments, shell movements alone were recorded from a large *T. derasa* (shell length, 45 cm) maintained in an outdoor running seawater table at the AIMS laboratory. The animal was covered by 2 cm of water at the midpoint of the siphon. A transducer was mounted on the side of the tank and attached by a small hook and rubber band to one of the valves. Measurements of valve gape were correlated with pen excursions on the chart recorder and found to be reasonably linear over the range of movements recorded (Fig. 1). Experimental results were obtained around midday on clear sunny days; during the course of an experiment radiant flux varied from 0.75 to 1.62×10^3 Einsteins/m^2/s, as measured with a Quantum Radiometer Photometer (Li-Cor). Shadows from a hand-held wand (a 7×14 cm rectangular piece of opaque plastic attached to the end of a 1 m dowel rod) were presented by passing the wand transversely across the posterior region of the siphon at the level of the inhalent aperture. The long axis of the plastic wand was parallel to the ventral margin of the shell and the characteristics of the shadow were maintained as constant as possible in terms of the location, velocity, and height (20 cm) of the stimulus. A photocell was positioned adjacent to the leading valve to monitor the onset of the shadow, and a barrier was erected to visually screen the experimenter from the animal's view and protect equipment from the resulting jets of seawater.
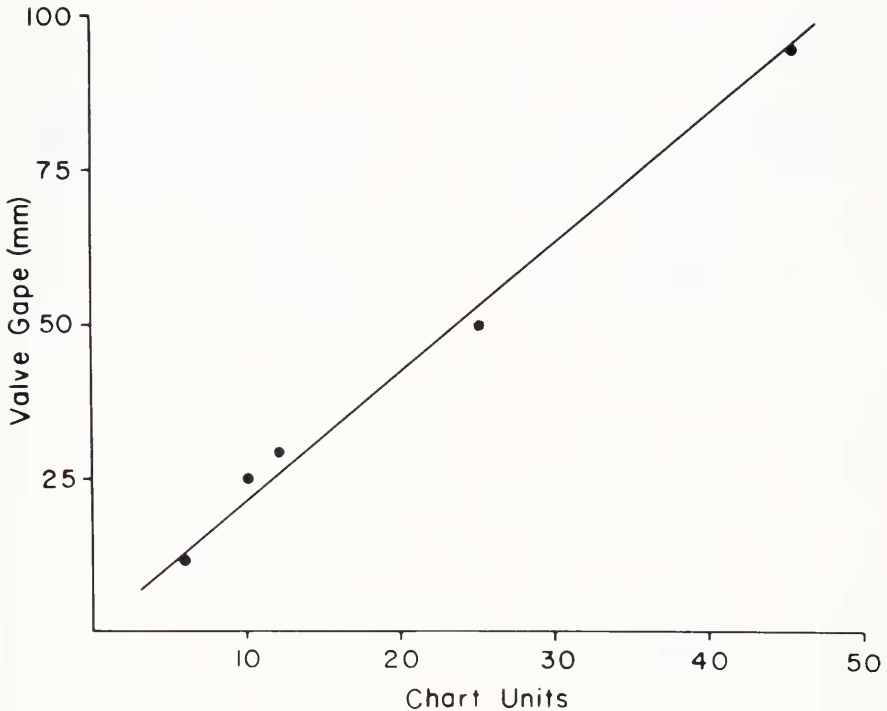
FIGURE 1. Calibration of strain gauge. Direct measurements of valve gape at the midpoint of the siphon in *Tridacna derasa* are plotted relative to pen movements. For a moderately large animal, with a shell length of 45 cm, maximum gape was 15 cm and the minimum gape, after considerable mechanical prodding, was 1.2 cm.

In other experiments, both shell and siphon movements were recorded from smaller *T. maxima, T. squamosa,* and *T. crocea* (13–18 cm) which were clamped by their left valve and suspended in a tank of aerated seawater in the laboratory. With this valve as the fixed reference point, shell movements were recorded from the right valve, as previously described, while siphonal retractions were recorded from the left side. A small wire hook inserted into the center margin of one of the siphon lobes was attached to a second transducer to record siphon movements. Overhead illumination was provided from a xenon arc source fed through a fiber optic light guide positioned 25 cm above the animal. An experimental 'shadow' was produced by closing an electronic shutter located between the light source and light guide.

Histology

A preliminary histological examination of the siphonal eyes was made by removing small pieces of the mantle followed by fixation in 10% formalin. Thick sections of plastic-embedded material were examined and photographed with a Zeiss Photomicroscope II.

RESULTS

General morphology of the siphon and eyes

The upper surface of *Tridacna* is composed of a series of deeply-curved siphonal lobes (Fig. 2) and an interconnecting mantle shelf. Each lobe is the greatly hypertrophied
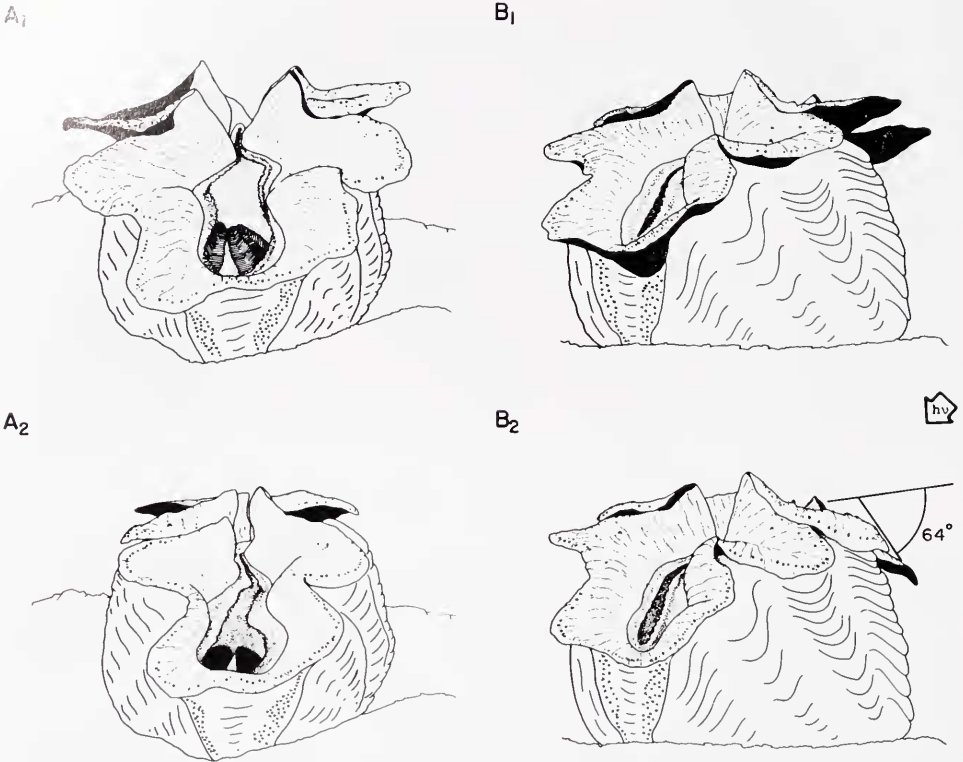
A$_1$

B$_1$

A$_2$

B$_2$

FIGURE 2.   Light-mediated siphon responses in *Tridacna maxima* (shell length, 10.8 cm) maintained in a laboratory aquarium, and viewed from the posterior region showing the inhalent aperture and gills. Drawings were made by tracing images projected from 35 mm color slides. The top figures (A$_1$, B$_1$) illustrate the fully extended posture of the siphon exhibited when the animal is exposed to direct sunlight. A symmetrical retraction of the siphon lobes typical of either the shadow response or sight reaction is illustrated in A$_2$. This is a synchronized response and is frequently coupled with valve adduction, although not in this instance, and with partial gill retraction. The orientation response is illustrated in B$_2$. An additional light source, positioned at an angle of approximately 45° from the right side of the animal, results in a lowering of the siphonal lobes which face the light. In this instance, the lateral surface of the siphon was lowered 64°, as indicated by an arc drawn relative to the position of the siphon in B$_1$. No other movements are associated with this response.

extension of the inner marginal fold of the mantle (Yonge, 1936) and these are extended laterally past the edge of the shell. The fullest extension of the mantle is observed in animals that occur below optimum depths, (R. D. Braley, pers. comm.). This posture is illustrated in Figure 2A$_1$ for a medium-sized *T. maxima*. In large specimens of *T. maxima,* and in the larger species (*T. derasa* and *T. gigas*), extension of the mantle past the shell margin does not increase in proportion to the size of the animal. Rather, the increase in upper surface area is associated with a deeper scalloping of the valves forming shell teeth, and the concomitant widening of the siphonal lobes. The interconnecting mantle shelf also assumes a greater proportion of the upper surface area in large animals.

The eyes, numbering in the thousands in large animals (Fankboner, 1981), are located primarily around the margin of the siphon (Fig. 2), and are readily distinguished in most animals by a concentrated ring of algal cells. A few additional eyes are located

on raised tubercles scattered over the mantle surface, although generally not on the interconnecting shelf region. The structure of the eye (see also Stasek, 1966) is that of an oblong capsule (Fig. 3A). The wall of the capsule is slightly constricted beneath the surface of the eye resulting in a fairly wide aperture. A layer of retinal cells lines the lower two-thirds of the capsule out of which an optic nerve extends into the adjacent tissues. Lens cells occupy the remaining interior portion of the capsule and are covered by a thin layer of epithelial cells at the surface. Each of the marginal eyes, whose orientation is indicated by the position of the lens and the contour of the mantle surface, faces laterally and above the plane of the siphon surface (Fig. 3B). Where the siphon is characterized by distinct, curved lobes, each eye is aligned with the radius of the lobe, a direction indicated relative to the radiating iridescent patterns of the animal as depicted in Figures 2 and 3B.

The varying orientation of numerous eyes effectively constitutes a type of mosaic visual system although considerable overlap occurs in the receptive field of the various eyes. This results in part from their location on adjacent folds of the siphon. In addition, the receptive field of each eye will be wide since the lens, in contact with the retina and having a refractive index presumably close to seawater, is not suitable for focusing and retinal cells extend well up along the sides of the capsule (Fig. 3A).

Shadow response behaviors

Local siphon retractions. The familiar visual response for which *Tridacna* is noted is the synchronous siphon retraction and shell adduction which results in a spout of seawater. A variety of visual stimuli can release this behavior. In contrast, slow local retractions of the siphon also exist. These are elicited only by shadows which cover a limited portion of the mantle such as a single fold, or a region bounded by as few as 3–4 eyes. To elicit this response, and avoid more vigorous siphon retractions, the shadow must approach the mantle edge gradually. The resulting indentation of the mantle in effect draws the siphon away from the shadow and reilluminates the tissue.

Local mantle retractions are the result of slow muscle contractions unlike the sudden movements characteristic of synchronous mantle retractions (*e.g.*, Fig. 4). Local responses may be due solely to peripheral interactions between receptor and effector systems, an hypothesis supported by the fact that similar responses occur in small isolated pieces of the mantle. Indeed, it is difficult to eliminate movements in a piece of mantle tissue containing a single eye. This was apparent while recording electrophysiologically from photoreceptors in the eye (Wilkens, 1984), where movements in response to dimming were a source of continual difficulty.

Synchronous retractions. A variety of synchronized responses are triggered by visual stimuli which involve retractions of the exhalent cone, of several lobes of the siphon, or the entire mantle surface, the latter often in concert with a partial adduction of the valves. An effective stimulus can range from direct shadows to visual stimuli producing the sight reaction. Responses exhibiting the greatest visual sensitivity, that is, to movements at a distance, are found in the cone-shaped exhalent aperture. These take the form of slight retractions, and/or an infolding of the lips. These movements occur independently, but also frequently precede the more vigorous siphon responses.

The extent of the visual response is determined in part by (1) the size and velocity of a moving object, as demonstrated by experimenting with animals in the field or in laboratory tanks, (2) the relative decrease in intensity of a controlled light stimulus, and (3) the behavioral state of the clam, a condition determined in part by the frequency of stimulation. In an undisturbed animal the threshold for a synchronized retraction of most or all of the siphon is low, although valve adductions frequently do not ac-

A
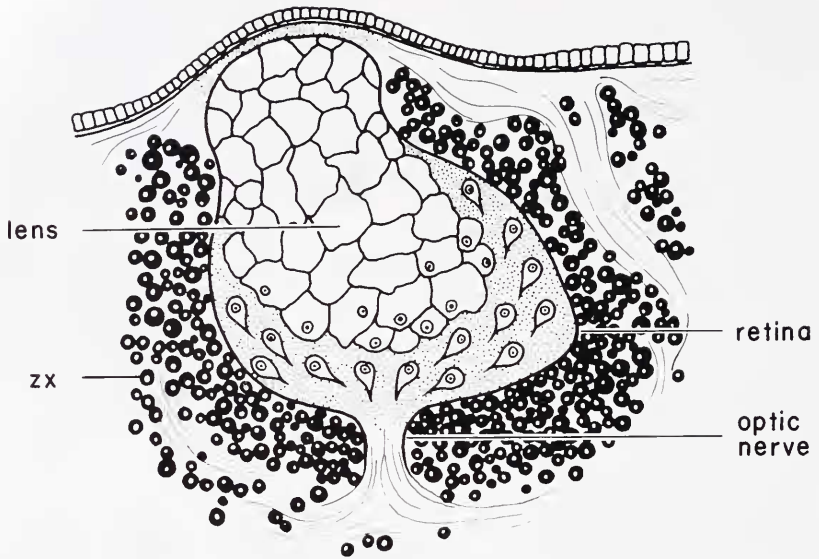
B

FIGURE 3. The eyes of *Tridacna* illustrated schematically in sagittal section (A, from histological sections), and in a piece of tissue freshly taken from the margin of the siphon in *T. maxima* (B). The morphology of the eye in A corresponds with previous results by Stasek (1966). Photoreceptors are shown with short processes extending toward the optic nerve as observed in anatomical studies with dye-filling of

company this response in the smaller tridacnid species. For example, no shell movement occurred in the visual response illustrated in Figure 2A.

Direct recordings of shadow response movements, including those of both the siphon and shell, are illustrated in Figure 4. A range of visual and spontaneous behaviors is seen. For example, a brief interruption of the overhead illumination may trigger only a partial siphon retraction and no shell movements (A, B). Occasionally, a partial siphon retraction (at arrow in C) will precede a more vigorous retraction and synchronous valve adduction which, in this instance, leads into a sequence of four synchronized siphon/shell movements. The visual response to a shadow, or shadow-like stimulus, therefore ranges from a partial siphon retraction to a sequence of vigorous movements, the latter signifying an elevated state of excitability. Spontaneous activity ranges from frequent slight twitches of the siphon to synchronous, near maximal movements of the siphon and shell (C) which occasionally obscure the visual response (Fig. 4A, at second shadow).

By contrast, a mechanical stimulus to the siphon nearly always triggers a rapid shell and siphon response (Fig. 4B). Even light brushing of the mantle produces valve adductions greater than those elicited by visual stimuli (*e.g.*, last trace, Fig. 5 where the amplitude is 40% greater). Records of valve adduction in the large clam at fast chart speeds (not shown) also show that the maximum rate of shell closure is more rapid (0.370 m/s) following a mechanical stimulus to the siphon than it is for shadow responses (0.275 m/s).

Muscle activity. An analysis of siphon and shell activity reveals that most movements are characteristically the result of sudden contractions which produce steeply rising recorded traces (*e.g.*, Fig. 4–6). The siphonal muscles along the margin of the outer folds are an exception in producing local retractions with a more gradual onset. The more distinctly organized bands of siphon retractor muscles which attach to the shell, and the single adductor, which is composed primarily of "quick" fibers (Yonge, 1980), are responsible for the respective rapid movements of the siphon and shell. The twitch-like contractions of the siphon retractors are present throughout the range of movement amplitudes observed and are likewise characteristic of both reflex responses and spontaneous movements.

Spontaneous siphon retractions occur over a range of amplitudes except in conjunction with spontaneous valve adductions where a full or near-maximum retraction is invariably observed (Fig. 4). Visual responses which elicit shell movements also trigger full retractions of the siphon. The endogenous nature of spontaneous movements is confirmed here by the behavior of animals housed singly in aquaria, and is associated with irrigation of the mantle cavity and periodic removal of feces and pseudofeces (Stasek, 1965).

Whereas both siphon and adductor muscles nearly always exhibit twitch-like contractions, the relaxation phase of these movements is quite variable. The siphon musculature relaxes more rapidly and in many instances reaches half-maximum amplitude prior to the onset of relaxation in the adductor muscle (Fig. 4A). Slower rates of siphon relaxation follow a mechanical stimulus (Fig. 4B), in contrast to those that follow

the receptor cells (author's unpublished results). Abbr.: zx = zooxanthellae. Three eyes from the marginal row are seen in B, plus a smaller eye located back from the edge of the siphon adjacent to the pin (0.4 mm in diameter) used to secure the tissue. The eyes face outward from the mantle edge; white arrows marking the position of the lenses are oriented parallel to the axis of each eye. Here, the eyes stand out from the surface in a slightly exaggerated fashion due to the partially contracted state of the tissue. Iridophores form radial bands (black arrows) parallel to the orientation of the eyes. A bubble of oxygen (lower edge) arises in response to strong illumination of the zooxanthellae from a microscope lamp.
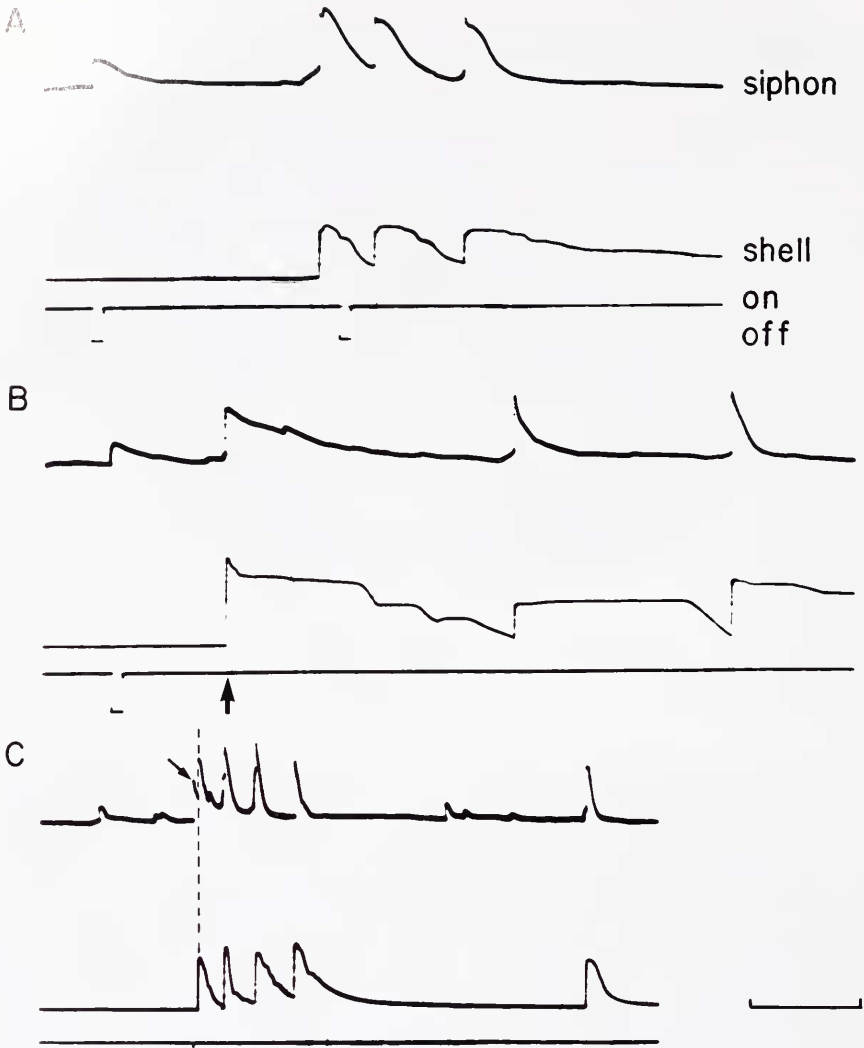
FIGURE 4. Movements of the siphon and shell in *Tridacna maxima*. (A) A shadow response followed by spontaneous activity. (B) A sustained contracture in response to a mechanical stimulus to the siphon (arrow) follows a shadow response. (C) Spontaneous activity and a sequence of vigorous activity following a shadow stimulus. Movements due to muscle contractions correspond to upward deflections in this and subsequent figures. A fiber-optic light source was located above the animal and its output controlled by an electronic shutter (monitored in the lower trace of each sequence). A vertical dashed line indicates siphon and shell movements in register in C. Time mark indicates 30 s (A, B) and 2.5 min (C).

spontaneous or visually evoked behaviors. A long-lasting retraction of the siphon occurs only when stimulation is sufficiently intense to cause substantial shell closure. The adductor muscle, on the other hand, frequently displays catch-like contractures as inferred from shell movements. The valves often remain stationary following adductions, particularly in response to tactile stimulation (Figs. 4B and 5, last record),
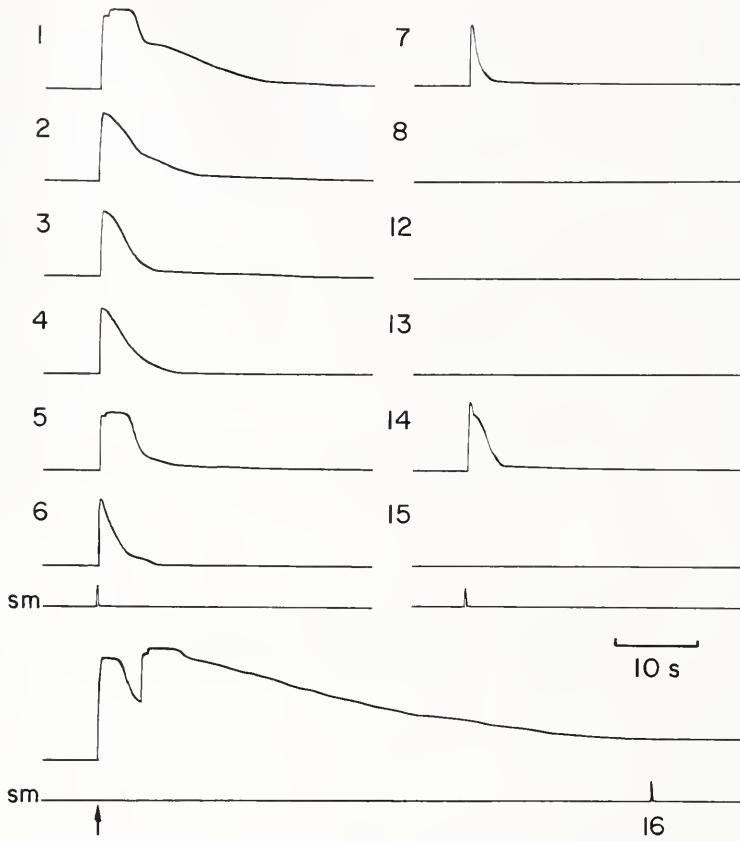
FIGURE 5. Shell movements in *Tridacna derasa*. This animal was maintained in an outdoor tank and received direct sunlight. Shadows were monitored by a photocell clamped near the edge of the shell. Stimulus monitor (SM) traces indicate the onset of shadows and a light tactile brushing of the siphon (arrow) in the bottom record. Traces are numbered according to shadows presented at two-minute intervals. Valve adductions were recorded for seven consecutive stimuli but did not occur in response to six additional shadows at the same location (trials 9–11 were omitted). In trial 14, the position of the shadow was moved to cover a different set of eyes. Trials 15–16 were at the original site.

and relaxation involves plateaus in the catch state as the valves reopen. It should also be noted that all of the valve movements recorded here can be attributed entirely to the adductor muscle, and not the pedal retractors. Through the byssus attachment and the fulcrum effect of the shell umbones, the pedal muscles exert considerable closing force when the clam is attached to its coral substrate (Stasek, 1965). However, in these experiments the byssus of *T. maxima* was attached only to loose gravel in the aquarium, while the larger *T. derasa* no longer possessed a byssus.

Habituation of the visual response. The shadow response of *Tridacna* habituates to repetitive visual stimuli. For example, animals found in shallow water do not respond to the constant flickering of light caused by surface waves (Stasek, 1965). To characterize the behavioral decrement, shell movements of a large *T. derasa* were recorded in response to shadows given at two-minute intervals. An example of an habituation test sequence is presented in Figure 5. The magnitude of valve adduction decreases gradually over successive trials in response to a constant stimulus, that is, to shadows affecting
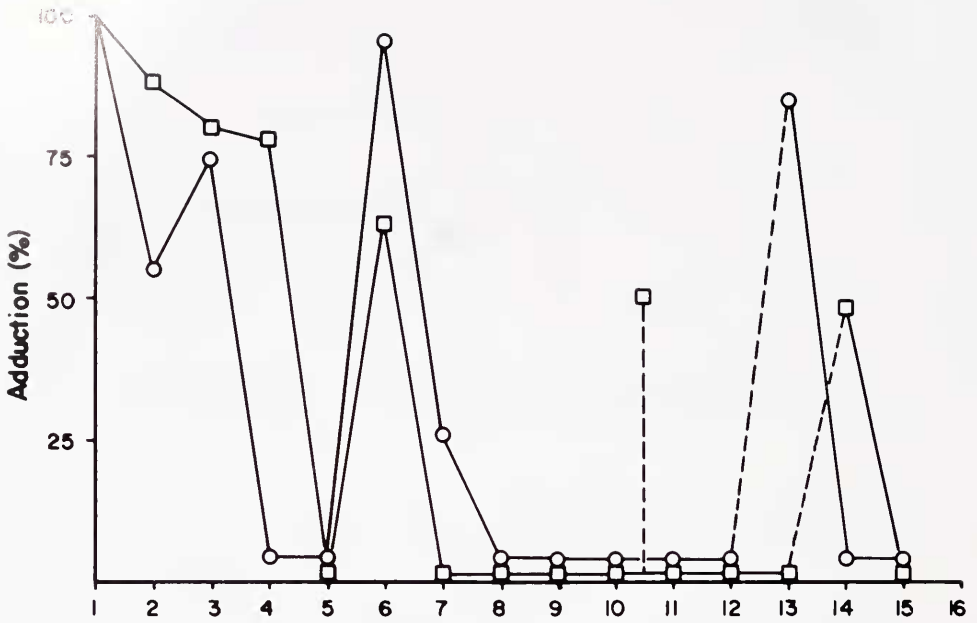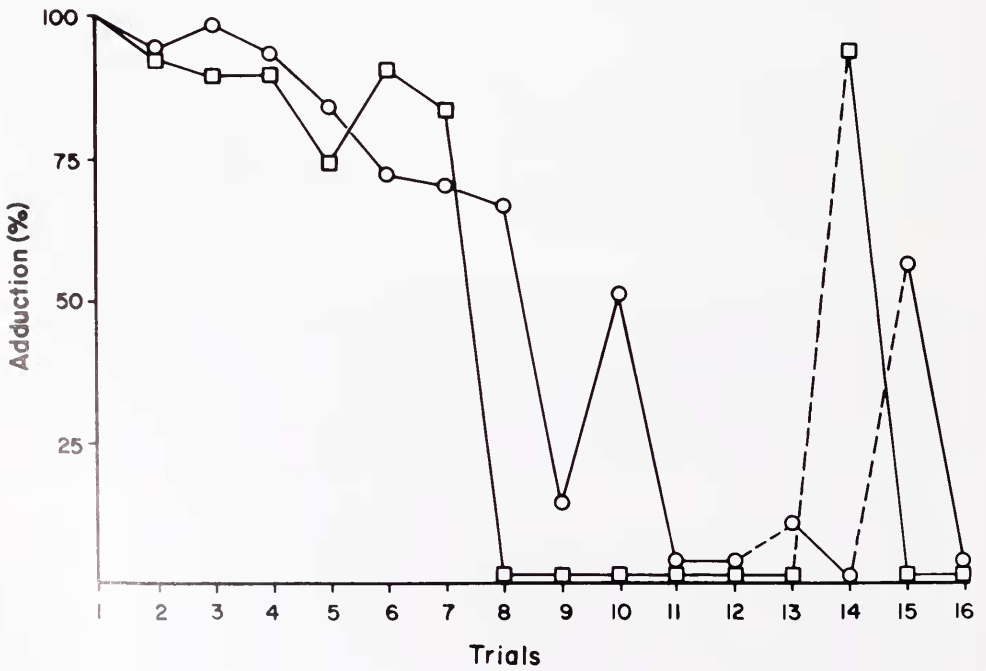
the same part of the siphon; the shell response eventually habituates completely (*e.g.*, by trial no. 8). Following the habituation of shell movements, however, shadow stimuli continued to elicit siphon retractions that produced jets of seawater, although these also became weak by trial no. 12. Shadow response valve adductions for four habituation test sequences are plotted in Figure 6. The decline of the response was similar for each of the two test sequences (separated by a 30–45 min rest period), although the number of trials eliciting a response varied from six to ten in this series of experiments.

Additional integrative features of the visual system were also apparent during these experiments. For example, the clam habituated to a shadow presented in one location responded vigorously when the eyes from another part of the siphon were shadowed. This effect is illustrated in two instances: (1) after trial stimuli no. 8–10 produced no response (Fig. 6A, curve □), the animal responded vigorously to the passing of a cloud (Fig. 7); (2) in all trial sequences a change in the location of the experimental shadow produced a vigorous valve adduction. A subsequent shadow at the original site was ineffective in each case. A change in duration of the stimulus is also effective in triggering a response (Fig. 6B, curve □, trial no. 14).

Orientation response

In bivalves, only sudden decreases in light intensity have been reported to trigger reflex behaviors—the familiar shadow response. *Tridacna,* however, exhibits a highly reproducible behavior in response to an increase in light intensity. This behavior is described based largely on observations of animals held in laboratory aquaria.

When illuminated under conditions ranging from full sunlight to fluorescent room lighting, an animal with expanded siphonal lobes invariably responds to an additional light stimulus by changing the orientation of its mantle surface relative to the incident light path. For example, light from a flashlight or fiber optic source directed toward one side of the animal will cause siphonal folds facing the light to curve downward. This response is illustrated in Figure 2B by drawings made from photographs taken before and 2 s following the onset of light. Each of the lobes facing the light has been lowered, in this case over an arc of greater than 60° relative to the initial posture (*cf.* Fig. $2B_1$–B_2). Although the entire lobe is affected, the response is most noticeable near the lateral margins where the change in position, up to 83.5° in one instance, results in the upper surface becoming approximately orthogonal to the direction of the additional light stimulus. The lobes on the side opposite the stimulus light do not respond. The directional component of the response can be further demonstrated by changing the position of the light source. In an anterior or posterior position along the midline of the animal, corresponding segments of each of the siphon lobes facing the light on both sides of the animal curve downward. The directionality of this response demonstrates the capability of the visual system for at least coarse spatial resolution.

In a few instances, a light stimulus will trigger a coordinated siphon retraction and partial shell closure instead of the orientation response. This is believed to be due to

FIGURE 6.   Habituation of the valve adduction response to shadows. On successive days, with results plotted separately in A and B, sequences of shadow stimuli were presented at two-minute intervals before (○) and following (□) a recovery period (30 min in A; 45 min in B). Upward broken lines indicate a change in shadow location from the site at which habituation occurred in A (curve □, no. 14; curve ○, no. 13) and B (curve ○, nos. 13, 15): in B (curve □, no. 14) the broken line indicates an increase in shadow duration. The vertical broken line in A indicates the response to a cloud (shown in Fig. 7). The second trial sequence (□) in B corresponds to results shown in Figure 5. All data are from the same animal.
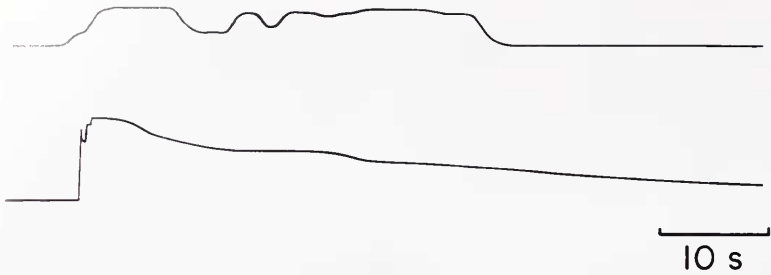
FIGURE 7. Shadow response in *Tridacna derasa* to the passage of a cloud (photocell monitor, upper trace). The change in radiant flux was 0.02×10^3 Einstein/m²/s; decreased flux is indicated by an upward deflection. Since *Tridacna* responds well to shadows controlled by a shutter, the "cloud response" is presumed to be due to a decrease in light intensity rather than a perception of movement by the cloud.

a difference in the state of excitability of the clam, with the defensive withdrawal response overriding the orientation behavior.

DISCUSSION

Behavioral adaptations

The shadow response. Giant clams are highly specialized bivalves, having evolved as hosts for internal photosynthetic symbionts in parallel with hermatypic reef-building corals. Their principal morphological adaptation is the hypertrophy of the mantle siphon which is positioned uppermost for exposure to light. Visually mediated behaviors are a major component of the protective mechanisms employed by *Tridacna*. Visual responses occur predominantly following a decrease in light intensity, either as the sight reaction or in response to direct shadowing. A characteristic of these behaviors is the twitch-like suddenness of both mantle retractions and shell closure. Since the siphon does not ordinarily retract completely inside the shell, the effectiveness of the response is due in part to a "startle effect" produced by the surge of water from the siphon apertures. This response is more forceably triggered by tactile stimuli, either to avoid or limit the extent of predation. The advantage of the visual response must therefore be to startle would-be predators at a distance, perhaps greater than that served by the water jet. Thus, it is hypothesized that the sudden movements of the large, brightly colored siphon constitute a visual component of the startle behavior. As described here, the rapid nature of siphon retractions and their frequent use independent of valve adduction supports this hypothesis. McMichael (1974) further suggests that the non-cryptic color patterns may serve to warn or confuse potential predators.

These visual behaviors are in sharp contrast to those of the scallop, another of the small number of bivalves with a well-developed visual system. Here, the onset of valve adduction is gradual due to selective activation of the slow, smooth-muscle component of the shell adductor (Wilkens, 1981). In tridacnids, where the mass of the adductor muscle is 85% twitch fibers (Maynard and Burke, 1971), as it is in the scallop, the shadow response includes activation of this fast component. Other bivalves also display sudden, light-mediated adductions (*e.g., Arca,* Braun, 1954; *Spondylus,* pers. obs.). The smooth adductor muscle in *Tridacna* nevertheless appears to be coactivated and is responsible for catch contractures characteristic of both visual and tactile responses. The stepwise relaxations and pre-contraction gaping movements (Fig. 4) suggest that

neural mechanisms for the release of catch may be similar to the plasticizing efferent control mechanisms in the scallop (Wilkens, 1981).

The orientation response. Bivalves in general are insensitive to a light-on stimulus with respect to short-term reflexes (Land, 1968), even though in some species (*e.g., Pecten,* Hartline, 1938; *Lima,* Mpitsos, 1973), light-on sensitive cells are represented equally in the pallial nerves with the light-off fibers presumed to be responsible for the shadow response (Land, 1968). The soft-shell clam *Mya* is an exception, reacting to an increase in light intensity by retraction of the siphon, although shadows produce a closure of the siphonal apertures (Wenrich, 1916; Hecht, 1918). The orientation response in the siphonal lobes of *Tridacna* is therefore one of the first examples of a bivalve reflex behavior triggered by an increase in light intensity.

The significance of this response is uncertain. One interpretation is that the siphon movements constitute a positive phototropic response that insures maximum absorption of light by the endosymbiotic algae. Phototropic behaviors also occur in the elysioid gastropods which retain symbiotic chloroplasts in their digestive tract and control light exposure by opening or closing the overlying parapodial flaps (Rahat and Monselise, 1979; Weaver and Clark, 1981). However, it is doubtful that a sudden light stimulus, equivalent to the experimental stimuli used in this study, would occur naturally in the environment of the clam. The reflex nature of the orientation response may therefore be a manifestation of the visual mechanisms which otherwise give rise to continual phototropic adjustments of the siphon. Any effect of light on the orientation of the siphon lobes would also depend on ecological factors such as depth, reef topography, and, perhaps, species. For example, *T. gigas* and *T. derasa* partially covered by coral outcrops orient their mantle surfaces toward available light (R. D. Braley, pers. comm.). Also, when these species are found lying on their side at the base of patch reefs and knolls, phototropic orientation of the siphon is evident.

Insofar as siphon orientation is related to illumination, the degree of siphon extension may also be visually mediated. At night the siphon lobes are partially retracted (Morton, 1978). With light adaptation, however, partial siphon extension develops along with sensitivity to shadows. During the day, the siphon is deployed with the valves widely separated. However, a total consensus on the degree of siphon extension during conditions of maximum insolation is missing. The greatest extension of the siphon in laboratory animals, equivalent to that depicted in Figures $2A_1$ and $2B_1$, occurred only when they were exposed to bright sunlight. Previously, Yonge (1936) noted that the "thickened mantle edges" were widely exposed even when only just covered by water. However, Braley (pers. comm.) has observed that, under the brightest conditions, animals located within 1 m of the reef surface do not extend their siphonal lobes as completely as those found at greater depths. Other invertebrates in the upper sublittoral environment that host zooxanthellae also partially retract their tissues in bright sunlight (Shick and Dykens, 1984; Mangum and Johansen, 1982; Porter, 1980), perhaps as a mechanism for reducing UV exposure (Shick and Dykens, 1984). Partial siphon retraction or a curling down of the lobes in *Tridacna* may also serve to decrease UV exposure. The eyes in *Tridacna* contain UV receptors (Wilkens, 1984), thereby establishing the sensory basis for this behavior.

Physiological mechanisms of visual behaviors

The visual system in *Tridacna* underlies a variety of behaviors including reflex responses to light and shadows. These behaviors raise interesting questions in relation to the physiological properties of the retinal cells. Unlike the scallop, which has pho-

toreceptors which generate spikes in response to shadows (hyperpolarizing) as well as light (depolarizing) (McReynolds and Gorman, 1970), *Tridacna* eyes contain exclusively hyperpolarizing photoreceptors, only half of which (S cells) produce axonal spikes in response to shadows (Wilkens, 1984). The presence of these off receptors is consistent with *Tridacna*'s predominant behavioral sensitivity to shadows.

More interesting is the fact that *Tridacna* apparently lacks photoreceptors equivalent to the depolarizing on-sensitive cells of the scallop, but yet has a direct behavioral reflex associated with a light stimulus, the orientation response. Regardless of whether this behavior represents a protective reflex or a positive phototropic response, it must originate from receptors which either fall silent when illuminated (S cells), or which synaptically influence second-order neurons in the retina. The latter alternative would provide a role for the non-spiking receptors (NS cells) which are equally represented in the retina (Wilkens, 1984). The remaining possibility is that extra-retinal photoreceptors, such as the "dermal" cells in the mantle edge of *Lima* (Mpitsos, 1973), are responsible for the direct light-sensitive responses in *Tridacna*. This is unlikely as the dermal photoreceptors in *Lima* are sensitive to dimming.

The neural circuitry of the visual system in *Tridacna* is also different from that of the scallop, the only bivalve from which there is sufficient information for comparison. In *Pecten* there are no peripheral synaptic interactions, either among the receptors in the eye (Barber *et al.,* 1967), or between optic fibers and neurones in the circumoral nerve ring (Spagnolia and Wilkens, 1983). In *Tridacna,* however, local contractions in response to dimming can be elicited in small pieces of the mantle isolated from the siphon. This requires the existence of peripherally located sensorimotor connections which also may be responsible for local siphon retractions. Synchronized movements of the siphon and shell are undoubtedly coordinated by the visceral ganglion which innervates the inhalent and exhalent regions of the siphon by separate pallial nerve trunks (Stasek, 1965), and the adductor muscle by additional motor nerves.

The scallop parietovisceral ganglion contains distinct lateral lobes (Dakin, 1910) which are devoted in large part to visual functions (Spagnolia and Wilkens, 1983). Whether equivalent functional lobes exist in *Tridacna* is not known. Nevertheless, several fairly complex visual behaviors are present in the giant clam. These include the ability to discriminate both spatial and temporal features of visual stimuli. Spatial integration is evident in several forms of behavior including the orientation response and the fact that animals habituated to a shadow at one location react strongly to changes in stimulus characteristics, *e.g.,* the unscheduled passing of a cloud during the test series, a situation which occurred on several occasions.

Sensitivity to the temporal characteristics of visual stimuli is illustrated again in animals habituated to periodic (2-min intervals) shadows. Here, vigorous reflex behaviors occur when the shadow becomes stationary. It is interesting that *Tridacna,* although extremely sensitive to moving objects, is also sensitive to a non-moving visual stimulus. Animals will react repeatedly to the interruption of an overhead light source (fiber optic light guide) that has no movement component. On the other hand, scallops respond poorly to non-moving stimuli such as a decrease in general illumination (pers. obs.).

Tridacna has evolved a unique and highly specialized visual system in association with its rather unusual hypertrophied siphon. The numerous eyes distributed along the siphon perimeter constitute a mosaic visual apparatus that is sensitive to shadows or movements in the vicinity of the animal. In addition, the visual system appears to mediate phototropic responses as an adaptation to the presence of symbiotic algae, and has the capability for discriminating spatial features of the environment. *Tridacna*

is also capable of aiming the exhalent jet of seawater in the direction of a tactile stimulus (Stasek, 1965), a response observed during the present study. McMichael (1974) hints that, with the exception of *T. gigas,* tridacnids are also able to aim exhalent jets on the basis of visual information. The capacity for spatial discrimination has been established in the present study, but whether *Tridacna* actually directs its siphon on the basis of a visual pattern awaits confirmation.

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